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Interacting effects of temperature, habitat and phenotype on predator avoidance behaviour in *Diadema antillarum*: implications for restorative conservation

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Abstract

Caribbean *D. antillarum* populations crashed following a mass-mortality event in 1983-4 with cascading effects on reef health. Population restoration efforts may be hampered by unknown effects of short and long-term elevated sea surface temperature (SST). We investigated how a key behavioural trait, predator avoidance behaviour (PAB; percentage of long defensive spines that moved in response to shadow stimuli), was affected by elevated SST in 180 individuals from two contrasting Honduran reefs; Utila (flattened reef structure, dearth of predation refugia), and Banco Capiro (complex reef structure, abundant refugia). Initiation of PAB is mediated by melanin, which breaks down at elevated water temperatures, so, as SST rises, *D. antillarum* may become vulnerable to predation. We compared local current SST (CSST; 29.7°C) with two IPCC predicted long-term climate change scenarios under laboratory conditions. PAB decreased by 13.98-15.37% at CSST +1.4°C and 31.67-42.44% at CSST +3.1°C. Trial temperatures were similar to maxima recorded in the Caribbean during the 2016 El Niño, therefore our results also represent likely responses to worst-case short-term acute temperature anomalies. Juveniles maintained higher PAB than adults, indicating increased reliance on anti-predation behaviours. White phenotypes from Utila's flattened reef maintained higher PAB than black counterparts, likely due to increased conspicuousness to visual predators. Habitat complexity may mitigate temperature-driven losses in natural behavioural defences. *D. antillarum* may be resilient to near-term (<2039) SST increases and periodic temperature stresses but may struggle under long-term, worst-case scenario conditions. Restoration of *D. antillarum* populations must be coupled to augmented reef complexity to improve future resilience.

Introduction

As architects of tropical reef ecosystems (Aronson and Precht 2001; Alvarez-Filip et al. 2009), much global attention is given to the impacts of elevated temperatures in driving the breakdown of symbiosis between scleractinian coral hosts and their photosynthetic zooxanthellae (Hoegh-Guldberg 1999; Kramer and Kramer 2000; Aronson et al. 2002; Sheppard 2003; Donner et al. 2005; De'ath et al. 2009; Cantin et al. 2010). However, acute and long-term temperature increases will also interact with other factors, such as habitat degradation, to affect other reef taxa (Przeslawski et al. 2008), and these effects remain largely unstudied.

Diadema antillarum, the long-spined sea urchin, is an important coral reef herbivore whose prolific grazing ability is essential for the maintenance of scleractinian coral domination throughout the Caribbean (Carpenter 1984; Liddell and Ohlhorst 1986; Macia et al. 2007). Between 1983 and 1984 a disease epidemic reduced populations by 95-100% (from 1.06-14.38m⁻² to <0.01m⁻²) across the 3.5 million km² area of the Caribbean (Bak 1984; Lessios et al. 1984a; Lessios et al. 1984b; Hughes et al. 1985; Lessios 1988ab; Levitan 1988; Carpenter 1990; Betchel 2006), and populations remain significantly depressed across the region to this day (Chiappone et al. 2002; Edmunds and Carpenter 2001; Weil et al. 2005; Debrot and Nagelkerken 2006; Bologna et al. 2012; Bodmer et al. 2015). This mass-mortality event is closely associated with macroalgal phase shifts and subsequent habitat flattening (Alvarez-Filip et al. 2009; Roff and Mumby 2012), which has decreased the availability of refugia (Alvarez-Filip et al. 2009) and potentially left *D. antillarum* vulnerable to predation. Models produced by Mumby et al. (2006) predict that *D. antillarum* population densities >1m⁻² are required for the maintenance of reef health throughout the Caribbean, therefore, augmentation of their populations, possibly through the deployment of artificial reef structures to replace lost habitat complexity, is a conservation priority throughout the region.

Under natural conditions, it is likely that *D. antillarum* is afforded a degree of environmental protection from predation by the complex structure of the reef (Ogden et al. 1973). However, individuals living on flattened contemporary Caribbean reefs with low percent cover of hard coral are likely to be more heavily reliant on direct predator avoidance behaviours; a role fulfilled by movement of their longest spines which have defensive barbs directed towards the distal end (Randall et al. 1964). Here, *D. antillarum* predator avoidance behaviour (PAB) is defined as the percentage of long predatory spines that move in response to a shadow stimulus. Decreases in light intensity, indicating the potential presence of a predator, evoke an excitatory response in the spines, making the individual hard to capture (Millott and Yoshida 1960a). However, PAB has an energetic cost and should be reduced in the absence of a predation threat (Millott and Yoshida 1960b), therefore increases in light intensity have an inhibitory effect on spine movement (Millott and Yoshida 1960a).

The underlying physiological mechanism for this behaviour is well understood: a layer of melanin-containing photosensitive melanophores, which give *D. antillarum* its characteristic black colouration, surrounds the test and enables changes in the light environment to be detected (Millott 1954; Millott and Yoshida 1959). This photic response is a direct result of interactions between light and the melanophore, as light stimuli cause expansion of the melanosomes, which in turn induces a nervous signal controlling spine movement (Yoshida 1956). However, melanin loses its structure at high temperature (Millott and Jacobson 1952; Sawhney 1994), suggesting elevated sea surface temperatures (SSTs) may cause a breakdown in these essential anti-predator light-detecting mechanisms.

Significant increases in SST are expected to occur on a decadal timescale and may reach values $>3.5^{\circ}\text{C}$ higher than current averages by 2100 (Collins et al. 2013). Additionally, the often catastrophic thermal anomalies of El Niño Southern Oscillation (ENSO) are also predicted to become biennial events of increasing severity by 2050 (Donner et al. 2005).

99 With a lifespan of up to 8 years (Randall et al. 1964), *D. antillarum* has relatively long
100 generation times, and their capacity to adapt to both long-term gradual, and short-term acute,
101 SST increases is likely to be limited. However, there is well documented phenotypic
102 plasticity associated with *D. antillarum* melanin production (Millott 1954), and numerous
103 ecological factors, such as wave exposure and water clarity, have been found to alter melanin
104 distribution and concentration within an individual's test and spines (Kristensen 1964). This
105 phenotypic plasticity may afford individuals with a degree of resilience to rising SST via
106 upregulation of melanin to counter breakdown associated with thermal stress.

107 We use laboratory manipulations on natural populations to investigate how *D.*
108 *antillarum* PAB is affected by increases in water temperature, and how this subsequently
109 interacts with habitat and phenotype. We compare two separate populations from contrasting
110 reef systems, representing both structurally complex and structurally simple 'flattened'
111 habitat types, in order to address whether habitat complexity influences PAB. Given that *D.*
112 *antillarum* colouration and light-detecting mechanisms are both controlled by phenotypically
113 plastic melanin regulation, we also explore whether PAB varies between phenotype (black-
114 and white-spined) and life-history stage (juvenile or adult) in relation to the individual's site
115 of origin. White-spined individuals are defined as adult urchins whose complete complement
116 of predatory defence spines are white in colouration. Theoretically, restoration of *D.*
117 *antillarum* is an obvious conservation target, however, to date, no studies have investigated
118 how they will respond to predicted environmental change. The results of this study will allow
119 conservation managers to gain better understanding of the interactions between PAB and
120 temperature, and make decisions on population restoration initiatives based on their future
121 survival potential.

Materials and Methods

Study sites

Data were collected on the Honduran island of Utila and nearby mainland reef system of Banco Capiro located within Tela Bay (fig 1). Full details of study sites can be found in Bodmer et al 2015. Banco Capiro (fig 2) has a mean scleractinian coral cover of 62%, which creates a structurally complex habitat that supports one of the highest contemporary *D. antillarum* population densities ever recorded. Utila (fig 3), by contrast, is a typical ‘flattened’ Caribbean reef system with low percentage scleractinian coral cover (15-20%) and consequently structural complexity is 25% less than at Banco Capiro (Bodmer et al 2015). Crucially, the abundance of key *D. antillarum* predators is similar between these two sites (Bodmer et al. 2015).

Future climate change predictions

The Intergovernmental Panel on Climate Change (IPCC) has recently described four new climate change scenarios, known as Representative Concentration Pathways (RCPs). Each RCP uses a different value of radiative forcing, dictated by the specific greenhouse gas (GHG) accumulation scenario being modelled, to predict the climatic changes that might occur by 2100 (Arora et al. 2011). Radiative forcing is measured in Wm^{-2} and is determined by the proportion of solar insolation that is trapped in the atmosphere relative to the energy radiated back into space and is, therefore, influenced by rates of GHG emission and accumulation (Van Vuuren et al. 2011). The four Representative Concentration Pathways (RCPs) are modelled on assumptions of socio-economic activity that are used to predict the

145 extent of GHG accumulation in 2100, and they have been designed to represent a range of
146 possible future climate change scenarios (table 1).

148 **Specimen collection and acclimatisation**

149 Trials were run between March and August 2015. 30 individuals in each of three
150 categories (black-spined adult, white-spined adult, juvenile; Fig 4) were collected from each
151 site giving a total sample size of 180 urchins over the six-month sampling period. Juveniles
152 were identified by their distinctive black and white banded spines, and their possession of a
153 test diameter <20mm (Randall et al. 1964). Four *D. antillarum* individuals were collected
154 each day by a combination of snorkelling and SCUBA, and trials conducted on the same day.
155 All individuals were returned alive to the reef within 24 hours of collection.

156 Pseudoreplication was avoided by collecting from a different sub-site each day. When
157 removing individuals from the reef, care was taken to ensure that minimal damage was
158 caused to the spines and test. Once an individual was located, a 50cm length of PVC pipe
159 (outside diameter = 2.6cm) was used to coerce them into the open. The PVC pipe was then
160 used to lift the individual off the reef and into a container for safe storage.

161 On returning to the laboratory, individuals were placed in to a 200L plastic holding
162 tank where they were allowed to acclimatise for a minimum of 8 hours before trials were
163 conducted. This short acclimatisation period was chosen to minimise stress and maximise
164 survivorship to reduce adverse effects on populations of this key reef herbivore. Thus our
165 trials tested the shock responses of *D. antillarum* to increased water temperature, and did not
166 account for the possibility of potential short or long-term adaptation/phenotypic plasticity and
167 our results must be interpreted in that light.

Experimental setup and climate change scenarios

Experimental manipulations were conducted in three transparent 64L plastic trial tanks. All tanks underwent 100% water changes daily with fresh seawater collected from the specimen collection sites. Aquarium filters (Eheim Pick Up) were installed in the holding tanks to maintain water quality overnight, but were not included in trial tanks due to the short time urchins were housed within them, and to ensure no external stimuli were present which may have influenced urchin responses. Aquarium heaters (AquaEl Easy Submersible Aquarium Heater 150w) and digital thermometers (Aqua One ST-3 Electronic Thermometer) were used to achieve and maintain the required water temperature in each trial tank.

Trial temperatures were based on recently described climate change scenarios from the Intergovernmental Panel on Climate Change (IPCC). They described four new scenarios, (Representative Concentration Pathways, RCPs), to predict the climatic changes that might occur by 2100 (Arora et al. 2011). Table 1 outlines the four RCPs, which range from a best-case scenario (RCP 2.6) to a worst-case scenario (RCP 8.5). SST increases are subsequently expected to range from 1°C (under RCP 2.6) to >3°C (under RCP 8.5) (Collins et al. 2013).

We used predicted SST increases for the Caribbean Sea/Gulf of Mexico under each RCP (Table 1; Hoegh-Guldberg et al. 2014), with one trial tank maintained as a control at 29.7°C; the current annual mean peak SST (CSST) recorded off the Caribbean coast of Honduras (<http://www.seatemperature.org>). Experimental temperatures were then calculated by adding predicted SST increases to this CSST. The second trial tank was used to represent an intermediate/stabilising pathway (RCP 4.5; 31.1°C), while the final tank was used to represent a worst case pathway (RCP 8.5; 32.8°C).

Having access to *D. antillarum* from both Utila and Banco Capiro also enabled us to evaluate whether the effects of rising SST are likely to be universal, or affected by the structural complexity of the population's site of origin. It is possible that temperature and site

interact to affect PAB, which has major implications for *D. antillarum* restoration initiatives aiming to provide artificial reef structure to stimulate recovery.

Trial protocol

Trials were conducted at night in a laboratory setting under artificial lighting maintained at an intensity of ca. 20 lm. The phenotype of each individual urchin was recorded and the total number of long defensive spines counted, along with individual weight (to the nearest mg) and test diameter (to the nearest mm) using long-jaw callipers. These measurements were recorded immediately after collection before individuals were placed in the holding tank to avoid inducing stress immediately prior to the trials. The predation avoidance behaviour (PAB) of each individual was then tested under each temperature scenario. Individuals were acclimated to each temperature for at least 30 mins before trials began, or until they had settled in a corner of the tank for a period of at least 10 minutes. This was done to ensure that urchins were adjusted to the heat shock and were therefore responding to the shadow stimulus and not the change in temperature.

At the start of each trial a GoPro Hero 3 underwater video camera was placed in the trial tank facing the urchin and set to record for the duration of the trial. Urchins were initially exposed to ambient light conditions for 30s. A shadow was then created over the urchin using an opaque wooden board to simulate the presence of a predator, and maintained for 30s before returning the urchin to ambient light. This was repeated three times for each urchin under each temperature scenario. The order in which individuals were exposed to the different temperature treatments was randomised ahead of each trial.

Quantifying predator avoidance behaviour (PAB)

Predator avoidance behaviour (PAB) was defined here as the percentage of an individual's total spines that move in response to a shadow stimulus, and quantified visually. Test diameter was measured in order to account for any confounding effect of body size on PAB. Only the movements of the longest spines were counted because the main function of these is known to be predatory defence whereas the shorter spines are used predominantly for feeding and locomotion (Randall et al. 1964).

Prior to their analysis, all 540 videos were renamed using RandomNames software. The video analyst was therefore unaware of the site of origin and climate change scenario of the urchin they were processing, thus removing any potential observer bias from the data. Video recordings were replayed in slow motion allowing accurate counts of the number of long defensive spines that moved in response to the shadow stimulus. The PAB for each simulated 'attack' was calculated and the means of these PAB values were used for statistical analysis.

Statistical Methods

PAB data were normally distributed and its relationships with climate change scenario, site and phenotype were analysed using a three-way repeated measures ANOVA with urchin number nested within climate change scenario. PAB was the continuous dependent variable, site and phenotype were nominal, fixed-effect between subject variables, and climate change scenario was a nominal, fixed-effect within subject variable.

We investigated the relationship between *D. antillarum* body size (test diameter) and PAB in order to control for this as a confounding variable, since smaller individuals are more vulnerable to predation, and predation threats are generally considered more relevant to juveniles than adults (Clemente et al. 2007; Jennings and Hunt 2010). All data were analysed using R.

243

244 **Results**

245 **Establishing a baseline PAB**

246 The mean PAB of black-spined adult urchins at CSST on Banco Capiro ($17.39 \pm 0.68\%$) is
247 used as a baseline for comparisons of different combinations of climate change scenario
248 (CSST, RCP 4.5, or RCP 8.5), site (Utila, or Banco Capiro), and phenotype (black, or white).
249 This is because black individuals on Banco Capiro are living in conditions that are most
250 similar to those under which *D. antillarum* existed prior to the mass-mortality event, i.e. they
251 are the most common phenotype, living within a dense population ($>2\text{m}^{-2}$) on a reef system
252 with a high percentage cover of hard coral ($>60\%$). There is debate in the literature about the
253 population densities under which *D. antillarum* evolved, and their relative importance as
254 macroalgal herbivores over evolutionary timescales has been called into question (Jackson
255 and Kaufmann 1987). However, countless studies conducted throughout the 20th century
256 clearly document high *D. antillarum* population densities, and demonstrate the importance of
257 this species for maintaining reef health on the overharvested Caribbean coral reefs of the
258 Anthropocene.

259 **Effects of temperature, site and phenotype on PAB**

260 There was a significant negative relationship between PAB and urchin test diameter
261 for juveniles ($F_1 = 4.993$, $p = 0.027$) but not for adults ($F_1 = 1.808$, $p = 0.18$) (Fig 5);
262 therefore, all subsequent analyses dealt with these two groups separately. Juvenile analysis
263 included test diameter as an independent variable while the analysis of adults did not.

264 Increasing water temperature caused a decline in PAB in both age categories of
265 urchins (Fig 6; Juveniles $F_2 = 4.86$, $p = 0.0091$; Adults $F_2 = 15.37$, $p = 3.9 \times 10^{-7}$) and

juvenile urchins had higher PAB than adults in all temperatures. Mean juvenile PAB declined from 24.54% (SE = 1.28) at CSST to 21.1% (SE = 1.45) under RCP 4.5 and 15.19% (SE = 1.22) under RCP 8.5. Repeated measures ANOVA revealed that there was no difference in PAB of juveniles between sites overall ($F_1 = 0.303$, $p = 0.58$) but the data for RCP 8.5 suggested lower PAB at Utila than Banco Capiro (Fig 6). Black-spined adult PAB declined similarly to juveniles from 17.66% (SE = 0.76) at CSST to 15.09% (SE = 0.9) at RCP 4.5 to 10.80% (SE = 0.87) at RCP 8.5. The percentage declines in PAB from CSST to RCP 8.5 were proportionately similar: 38.1% for juveniles and 38.8% for black-spined adults. Interestingly, PAB of juveniles under RCP 4.5 was still 21.33% higher than that of black-spined adults under CSST.

There was no evidence of between-site differences in PAB or its response to temperature for black-spined adult urchins but the pattern differed for white-spined adults, reflected by a significant interaction between phenotype and site ($F_1 = 8.96$, $p = 0.003$). White urchins from Banco Capiro ($14.35 \pm 0.58\%$) displayed lower PAB than those from Utila ($19.50 \pm 1.34\%$), and mean white urchin PAB on Banco Capiro ($14.35 \pm 0.58\%$) was lower than that of their black counterparts ($17.39 \pm 0.68\%$). However, the inverse was true on Utila where mean white-spined adult *D. antillarum* PAB ($19.50 \pm 1.34\%$) was higher than that of the black population ($17.93 \pm 0.84\%$). However, these differences were less apparent at RCP 8.5 (Fig 6). At CSST mean PAB of white-spined adults on Utila (19.50%, SE = 1.34) was almost 36% higher than those on Banco Capiro (14.35%, SE = 0.58). This difference was maintained at RCP 4.5 (15.49%, SE = 0.91, and 11.20%, SE = 0.47 respectively) but was roughly halved at RCP 8.5 (11.44%, SE = 0.92, and 9.70%, SE = 0.49). See table 2 for complete breakdown of results.

Discussion

Demographic influences on PAB

At CSST, mean juvenile PAB is 41.12% greater than black-spined adults on Banco Capiro, and the higher PAB value is maintained even under moderate thermal stress (RCP 4.5). This is not surprising, as juvenile test diameters are typically smaller than the 40mm predator escape threshold above which vulnerability is believed to decrease (Clemente et al. 2007; Jennings and Hunt 2010). The need for juveniles to maintain high PAB, even under physiological stress, is far greater than for their adult counterparts. This is supported by the negative relationship observed between juvenile body size and PAB magnitude; larger juveniles can partially relax PAB in favour of the energetic benefits associated with reduced spine movement (Millott and Yoshida 1960b). However, juveniles living within the complex structure of Banco Capiro still maintain similar PAB to those on the flattened reefs of Utila, despite potentially being able to gain energetic benefits from reducing PAB on a reef that provides individuals with environmental protection. The risk of death under any given attack is much higher for juveniles than adults, and thus the energetic benefits of reducing PAB on Banco Capiro are likely to be outweighed by the ultimate price of failing to respond to a potential predation threat.

On Banco Capiro, white-spined adult *D. antillarum* individuals have a significantly lower PAB than black-spined adults. One possible explanation relates to the developmental and environmental processes driving these phenotypic differences. Experimental manipulations have shown that adult *D. antillarum* will develop white spines if reared in low-light environments, while also favouring shaded areas of reef during adulthood (Kristensen 1964; Groun 1989). Due to reduced energy content in algae growing on shaded compared to light-exposed reef areas (Carpenter 1985; McCook et al. 2001), white-spined adult sea

urchins are likely to be nutrient-limited and may therefore be unable to invest in metabolically expensive melanin production. Whilst white-spined adults appear to be less sensitive to predation stimuli, their overall vulnerability may be unaffected by this decreased PAB ability because they favour shaded, and presumably more complex, habitats.

Conversely, juveniles develop black spines when reared in high-light environments (Kristensen 1964), typically when individuals settle on more exposed areas rather than within the complex coral framework. It is therefore likely that black-spined adult *D. antillarum* are grazing algae from light exposed reefs that have greater energy availability per unit area (Ogden and Lobel 1978) than their white-spined counterparts. Black-spined individuals may therefore be able to invest more heavily in melanin production. This investment in their light-detecting sensory systems is further justified in black-spined adults because their more exposed lifestyle leaves them vulnerable to predation.

For black-spined adults and juveniles the magnitude of PAB does not differ between sites, but for white-spined adults PAB is significantly greater on Utila. Unlike on Banco Capiro, white urchins on Utila are living in a flattened habitat and therefore lack abundant predation refugia. The major fish predators of *D. antillarum* (Ballistidae, Haemulidae and Labridae) all possess typical vertebrate visual systems comprised of image-forming eyes (Lamb et al. 2007), which rely, at least partially, on contrast for prey detection (Schuster et al. 2011). Against the darker backdrop of the reef, white individuals are likely to be more conspicuous to predators in a habitat where they are less able to hide. Therefore, while black individuals on Utila are less conspicuous to predation, and both adult phenotypes on Banco Capiro are afforded environmental protection by the reef structure, white-spined adults on Utila must invest more heavily in the maintenance of their innate behavioural PAB.

Elevated SSTs and their implications for restoration

Across all combinations of site and phenotype, mean *D. antillarum* PAB was negatively affected by increases in water temperature, with the greatest reductions under the most extreme temperature trials (RCP 8.5). This suggests that *D. antillarum* is likely to become increasingly vulnerable to predation as climate change progresses, especially if ‘worst case’ temperature models arise. Subsequent increased predation vulnerability will further hinder population recovery from the 1983-84 mass mortality event, and potentially hamper current conservation initiatives as seas warm. We find that, under RCP 8.5 conditions, *D. antillarum* PAB will be reduced by between 32.44% and 41.33% relative to CSST. However, it is generally accepted that RCP 4.5 is a much more likely future temperature scenario (Masui et al. 2011; Thomson et al. 2011). According to our results, under RCP 4.5, smaller PAB decreases of between 14.55% and 21.95% will be seen; although this still represents a significant loss of anti-predation capability in such a threatened species.

Unfortunately, our results indicate that juvenile urchins will be similarly affected by rising SST as black-spined adults. Given that juveniles are more vulnerable to predation due to their small size below the predation threshold (Clemente et al. 2007; Jennings and Hunt 2010), it is likely that this decrease in PAB will translate into elevated mortality rates among younger cohorts. Previous research has already identified maturation as the key life history bottleneck to *D. antillarum* recovery (Williams et al. 2010 & 2011; Bodmer et al. 2015), meaning any further reduction in juvenile survival will ultimately drive Allee effects and eventual extinction. However, it is important to remember that this study has tested responses to sudden and acute thermal stress, using similar approaches to much other ecophysiology research, e.g. Eme and Bennett (2009), Eme et al. (2001) and Dabruzzi et al. (2012), and thus our results do not account for phenotypic plasticity associated with the *D. antillarum*

melanin-regulatory system (Millott 1954). This may serve to mitigate the negative effects of rising SST on PAB, meaning this study represents a worst-case scenario and not the end of the road for conservation efforts throughout the Caribbean.

It is also important to consider the temporal scale over which ocean warming will actually occur. We show that under the long-term water temperatures predicted by RCP 4.5 (CSST +1.43°C), *D. antillarum* will likely be partially resilient with respect to the detection of, and reaction to, predators. With long-term temperature increases under RCP 4.5 greater than short-term increases under RCP 8.5 (CSST +0.83°C), we can assume that *D. antillarum* will be resilient to near-term SST increases across the severity range. This suggests that, at least until 2039, incremental ocean warming is unlikely to negatively impact the success of *D. antillarum* restoration initiatives.

However, increases in the frequency and severity of El Niño anomalies means that long-term warming is not the only thermal threat to be faced. In winter 2016, average Caribbean SST was 0.5-1.5°C higher than the 1981-2010 average (NOAA). Fortunately, our focus on acute temperature increases, similar to those experienced during El Niño, indicate that *D. antillarum* will be able to maintain PAB provided that sudden increases do not exceed ~3°C. In general, the severity of El Niño in the Caribbean is less than other global coral reef hotspots, and this ~3°C threshold falls outside the temperature anomalies previously experienced in the region (NOAA).

It has been suggested that *D. antillarum* conservation efforts should focus on reintroduction coupled with artificially augmented structural complexity (Bodmer et al. 2015). Our results suggest that conservation interventions seeking to increase structural complexity will reduce the reliance of *D. antillarum* on innate behavioural PAB, and increase survivorship even in the face of worst-case scenario increases in SST. In essence, structural

complexity may provide a buffer against the increased threat of predation caused by reduced PAB via melanin breakdown. Stakeholders can use this information to make informed decisions about strategies to increase the health of Caribbean coral reef ecosystems by focusing on this important species. This is in line with the IPCC's goal of "working with scenarios...in order to consider how robust decisions or options may be under a wide range of possible futures" (Moss et al. 2010). Our results indicate that, if *D. antillarum* is going to recover and aid the reversal of ubiquitous macroalgal phase-shifts, they require urgent conservation attention to be buffered from climate change induced thermal stressors.

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558 Table 1. Data extracted from table SM30-4, section 7 “Coral Reef Provinces”, row 1
559 “Caribbean Sea/Gulf of Mexico” (Hoegh-Guldberg et al. 2014).

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Climate Change Scenario	Predicted near-term (2010-2039) increases in SST (°C)	Predicted long-term (2010-2099) increases in SST (°C)	Pattern of radiative forcing value increase	Likelihood of occurrence
RCP 2.6 (best-case)	0.48	0.68	<ul style="list-style-type: none"> • Mid-century peak at 3.1Wm^{-2} • Decrease to 2.6Wm^{-2} by 2100 	<ul style="list-style-type: none"> • Unlikely • Requires immediate GHG emission reduction on a global scale
RCP 4.5 (stabilising)	0.64	1.43	<ul style="list-style-type: none"> • Rise to 4.5Wm^{-2} by 2100 • No further increases 	<ul style="list-style-type: none"> • Moderately likely; radiative forcing peaks in 2040 and then plateaus • Would require immediate cooperation and coordination between the world's governments
RCP 6.0 (stabilising)	0.61	1.87	<ul style="list-style-type: none"> • Rise to 6.0Wm^{-2} by 2100 • No further increases 	<ul style="list-style-type: none"> • Most likely; radiative forcing peaks in 2080 and then plateaus • Pressure put on governments to address climate change issues will likely cause GHG emission reductions, but time is required to coordinate the effort
RCP 8.5 (worst-case)	0.83	3.14	<ul style="list-style-type: none"> • Rise to 8.5Wm^{-2} by 2100 • Continue unabated into 22nd century 	<ul style="list-style-type: none"> • Unlikely • Requires GHG emissions to continue at current rates; concerted efforts are already being made to reduce them

574 Figure 1. Site map showing the locations of Utila and Tela Bay, Honduras.



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576 Figure 2. Landscape photograph of Utila showing ‘typically’ low hard coral cover and

577 associated lack of habitat structure. Photo credit: Adam Laverty.



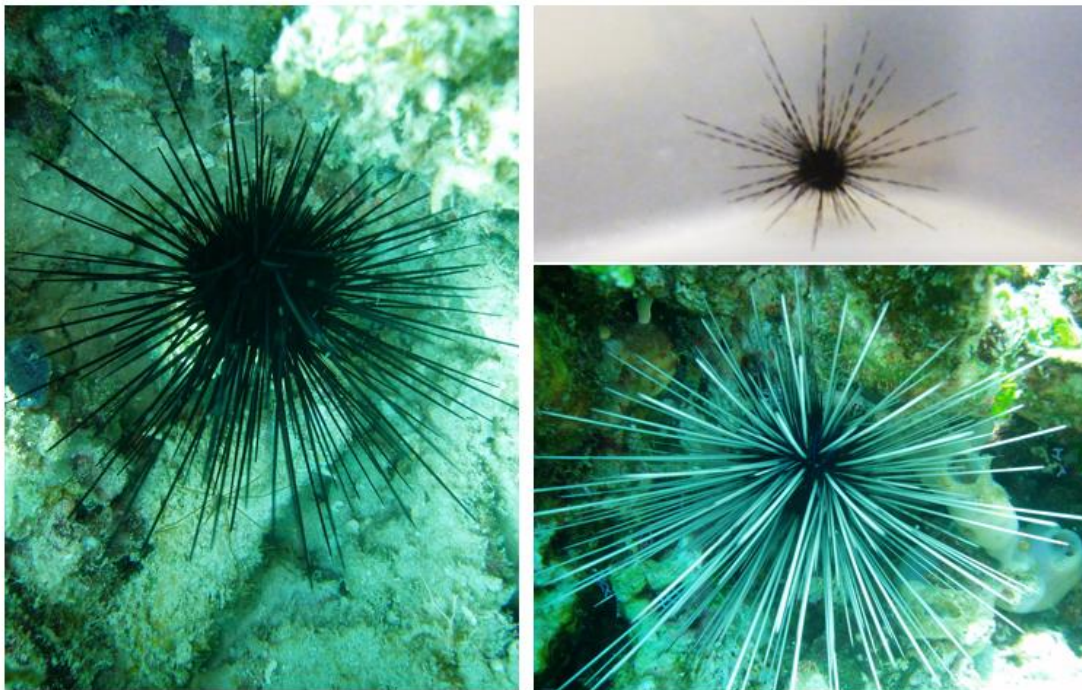
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579 Figure 3. Landscape photograph of Banco Capiro showing the high percent cover of hard
580 coral and resultant architectural complexity. Photo credit: Dan Exton.



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582 Figure 4. Panel photograph of *D. antillarum* adult and juvenile phenotypes. Far-left = black-
583 spined adult, bottom-right = white spined adult, top-left = juvenile.



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Figure 5. Relationship between urchin body (test) size and predator avoidance behaviour (PAB) in juvenile (black points) and adult (grey points) urchins. Plotted lines are least-squares regression lines.

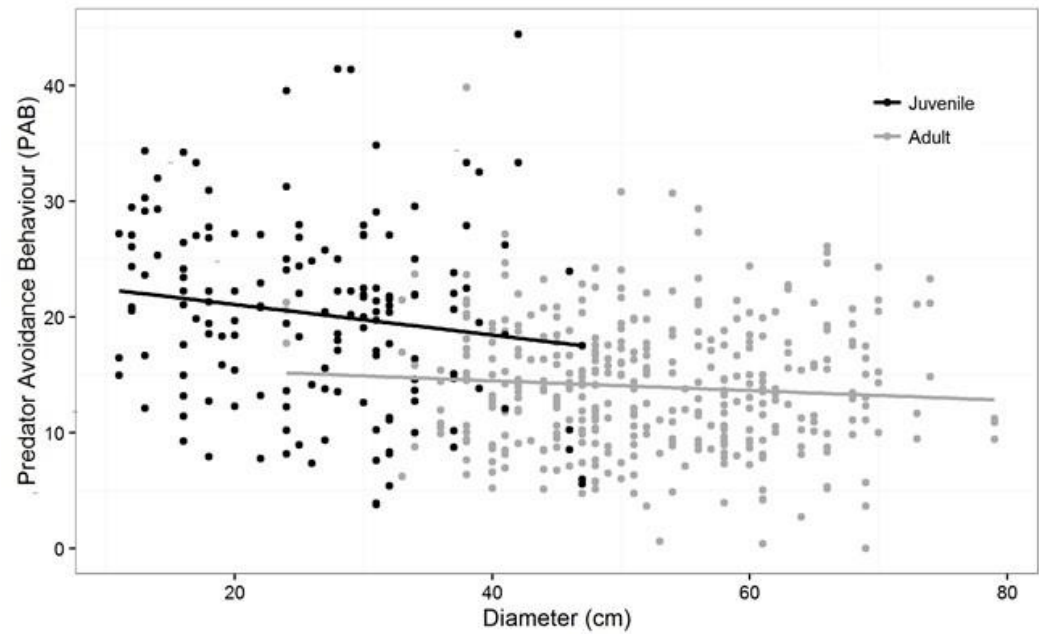


Figure 6. Predator avoidance behaviour (PAB) of *Diadema antillarum* of three categories (black-spined adult phenotype, white-spined adult phenotype and juvenile), across two sites (Utila: flattened reef and Banco Capiro: complex reef), under conditions simulating three different IPCC climate change scenarios (CSST = 29.7°C, RCP 4.5 = 31.13°C, and RCP 8.5 = 32.84°C). Grey horizontal lines represent a baseline for comparison set as the mean PAB of black-spined adult *D. antillarum* on Banco Capiro under CSST. Vertical lines represent ± 1 SE.

